CONTRIBUTIONS TO OUR KNOWLEDGE OF THE ANATOMY AND RELATIONSHIPS OF SPIDERS.

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INTRODUCTORY REMARKS. TERMINOLOGY.

Walckenaer may have been right when in 1837 he pointed with pride to the long list of works on spiders already in existence and said that if Pallas could only see it, he would surely no longer reproach naturalists for neglecting this interesting group of animals. Unfortunately the reproach of Pallas may be repeated now more justly than ever before. It is true that a quantity of excellent work has been published since the time of Walckenaer, much more and much better work than before. But the group remains a neglected one especially if compared with such favorites as insects or vertebrates. When two years ago I began to gather material for a manual on spiders I soon became aware that our knowledge of their anatomy and embryology is entirely inadequate. Not only the nervous system and the sense organs, but even the external sexual organs from which the characters for the identification of species are chiefly derived need thorough re-examination. This sad discovery stimulated me to new research and the present series of articles is a result of it. I shall omit all reference to literature which will be extensively treated in the manual I hope to be able to complete and to publish some day. Only such papers will be mentioned as are absolutely necessary to the understanding of the subject. Moreover to avoid loss of time and to make the reading easier I shall describe things as I found them during my investigations, without making constant mention as to what is new and what was already known. Those who know the literature will easily separate the new from the old, while those who are not so well acquainted with it will be glad to have the subject treated in a short and comprehensive manner. I need scarcely add that everything described by me in the present series of articles is based on careful and extensive study.

Concerning the methods I have applied during my investigations I have little to say. They are the ones commonly used by zoologists and anatomists, i. e., dissecting with the aid of scissors, scalpels and needles for macroscopic examination, at times aided by in toto staining and injections; mounting of whole spiders or parts in canada balsam, glycerin or some other medium; and finally sectioning with the microtome after applying the usual reagents. Used alone none of those methods is quite reliable. But when one is controlled by the others and when the number of specimens and forms studied is sufficiently great, one gets a clear idea of relations which would otherwise entirely escape observation.

To one point I desire to call particular attention. The terminology in this group is in as bad a shape as in any other group of animals. Even the names for the three planes of the body have not found universal acceptance in their application to the different groups of the animal kindgom and what is still worse the same term has often more than one entirely distinct application. Thus the term TRANSVERSE plane is used by different authors to designate each of two separate intersecting planes, which results in terrible confusion. In the case of appendages the terms upper and lower, anterior and posterior, internal and external have also been applied to the same structures, making it at times extremely difficult to understand the author's exact meaning. To avoid all misunderstanding I shall therefore give in this introduction the terms as I will use them throughout the entire series of articles as well as in my papers on systematics, the first of which will be ready for print in the near future. Whenever possible I preferred new terms to old ones, not out of desire to augment the number of terms of which there are already more than needed, but to enable the reader to know at once and exactly their meaning. Some of these terms are cumbersome and possibly could be replaced by better ones. However, clear and exact terms are in my opinion to be preferred to those which although easily remembered are at the same time easily confused.

The three determining planes of the body, applying to all animals I will call as follows:

1. THE PLANE OF SYMMETRY (called usually the sagittal or chief plane). It divides the body into two symmetrical parts, and not only in arthropods but even in echinoderms and coelenterates there is only one plane of symmetry. All planes that run parallel to it I will call *parasymmetrical*.

2. THE SYNAXONIAL PLANE (called often the frontal, and by Claus and others wrongly the transverse plane) is a plane intersecting the plane of symmetry at right angles in such a manner that their line of intersection forms the chief axis of the body

or the *axis of complex symmetry*, if I may use a term accepted in crystallography. The position of the synaxonial plane in coelenterates and echinoderms is quite exact since the chief axis itself is determined by the points of intersection of the radii. In Arthropods in which the axis is not exactly determined by the structure of the body itself, we may accept as the synaxonial plane, the plane which divides the tergites from the sternites. In the case of spiders it is the plane which separates the cephalothorax from the sternum. Any plane parallel to this plane I will call *parasynaxonial*.

3. THE DIAXONIAL PLANE (usually called the transverse plane) is a plane intersecting the former two (and the chief axis) at right angles. Any plane which does this is a diaxonial or transverse plane.

An exact terminology may be derived from these terms for the different planes, surfaces and edges of appendages, such as legs, antennae, palpi, chelae, etc., since all these are built on the principle of bilateral symmetry. In consequence they have all three determining planes of their own. Such terminology is especially important in systematics. To comprehend the new terms clearly, one must imagine all legs as growing out of the sides of the animal at a right angle to its chief axis and the chelae and mouthparts as parallel to it. (Fig. I.) For the sake of convenience we may drop the prefix "para," since this does not impair clearness. As will be easily understood from an examination of the diagram, the terms apply to both sides of the body equally well, so that it is not necessary to mention "left" or "right" and yet no confusion can result. The same term applies to a surface whether it be a leg of a mammal or of a spider, whether a front or a hind leg.

1. THE EPISYNAXAIL SURFACE (should be epiparasynaxonial) commonly called "dorsal." The term dorsal is however objectionable since the articulation of the limbs is frequently such that the episynaxial surface is not really dorsal in position, as for example in the crabspiders.

2. THE HYPOSYNAXIAL SURFACE (should be hypoparasynaxonial) commonly called "ventral," the latter name being objectionable on the same ground as "dorsal." The terms dorsal and ventral I will apply to the body only, not to the appendages.

3. THE PROSYMMETRICAL SURFACE (should be proparasymmetrical) is the lateral surface nearest to the anterior end of the

chief axis of the animal (Fig. I. pro). It corresponds therefore to the "inner" surface of the front legs, or to the "outer" surface of the hind legs in spiders. It also corresponds to the "inner" surface of the chelae in Theraphosidae called "anterior" in true spiders.

4. The Retrosymmetrical Surface (should be retroparasymmetrical) is the lateral surface nearest to the posterior end of the chief axis of the animal. It corresponds to the "outer" side of the front legs or to the "inner" side of the hindlegs. (Fig. I. retro). In the chelae it corresponds to the "outer" surface Theraphosidae, or "posterior" in true spiders.

The four edges or lines of intersection of the four surfaces mentioned in those cases when the appendages are not cylindrical in form may be called "epipro" (Fig. 2. ep), "epiretro" (Fig. 2, er), "hypopro" (Fig. 2, hp) and "hyporetro" edge, and the middle lines or the lines of intersection of the three determining planes with the four surfaces mentioned may be called the upper and lower, pro and retro middle line. In the case a structure or edge is oblique as the margins on the chelae for example, it may be simply designated by the word pro or retro. Thus the "marge inferieur" of Simon's terminology, called by Banks "the row behind the fang" and by Montgomery "the posterior margin" is according to my terminology the *Retro*margin; while the "marge superieur" of Simon or the anterior margin of Montgomery is the *Pro*margin. There can be no confusion if we apply this terminology consecutively, no matter what the actual position of the limb, if we only remember that each limb has only one plane of symmetry and that the entire terminology is based on the correlation of planes and their homology in the left and right side of the animal.

I. The Structure and the arrangement of hair on the legs of Pholcus phalangoides Fussl.

Little attention has been paid to the hair covering the legs of spiders. This is deplorable since many a valuable character may still be derived from its study, as the investigations of Dahl on the trichobothria have proven. They are of great help in the separation of families although their value should of course not be overestimated. I do not know whether the hair will eventually furnish characters of value for the separation into genera, but it has been already applied for the separation into species of the genus Latrodectus and it certainly will help to establish relationships between forms which would otherwise remain separated in the system.

While studying the muscular system and articulations in Pholcus I was struck by the regularity of the rows of hair on the legs. A comparison of many specimens showed that this is a constant character. The leg has not the form of a perfect cylinder, but shows in a cross-section a circle with flattened sides, represented diagrammatically in Fig. 2. There are in all 8 rows of hair; two rows on the episynaxial surface (esp and esr), one on the middle pro (mp) and one on the middle retro line (mr), and four rows on the four edges (ep, er, hp, hr). We find the same arrangement on each segment of all legs beginning with the femur; but the tarsus of the fourth leg in both sexes has a ninth row of hair on the middle hypo line. The onychium of each tarsus is surrounded in all legs by 8 bristles, two of which are unpaired and belong to the tarsus. The structure of these bristles may best be understood from the drawing. (Fig. 4.)

The hair forming the eight rows on the femur and tibia is of uniform structure. It is represented in Fig. 5, in its entire length and a part of it on a larger scale in Fig. 6. It is characterised by the spiral row of small spines reaching a little beyond its middle. Each hair is inclined towards the distal end of the limb at an angle of from 27–30 degrees. In a female of 2 mm. cephalothorax length the hair on the femur marked in Fig. 2, with the letters *esp* and *esr* is about 0.8 mm. long, while that forming the other four rows is only 0.57 mm. long. In the tibia all rows consist of hair of the average length of 1.0 mm. There are no trichobothria on the femur and tibia, but on the latter are some six or seven extremely small hairs without any special structure, measuring about 0.06 mm. The hair of the metatarsus is considerably shorter than that of the tibia, but still of the same structure in its proximal two thirds. The longest hair is at the base of the metatarsus measuring in the above individual 0.4 mm. Towards the distal end of the metatarsus the hair becomes gradually shorter and changes structure. It measures now only about 0.28 mm. loses the spiral of small spines, while the two basal spines—the only ones remaining—become considerably stronger. (Fig. 7.) There are besides some six or seven scattered hairs measuring about 0.12 mm., simple at the proximal end of the segment and toothed at its distal end, where it looks as represented in Fig. 11. This hair may be bent anteriorly or erected more than the common hair. Its teeth are directed away from the tip of the limb. Similar hairs, only shorter and with longer teeth are found on all tarsi, about one dozen in number (Fig. 10). The hair forming the eight rows on the tarsi is of the same structure as that at the distal end of the metatarsus, but also smaller, measuring from 0.2–0.28 mm. and with stronger basal spines (Fig. 8) to which two more are sometimes added. The fourth leg in both sexes has besides, as already mentioned, a ninth row of specially structured hairs. They occupy the hypomiddle line and are from thirty to thirty-four in number. They have hooks on one side and little spines on the other (Fig. 9) and are so arranged that the spines are directed distally towards the tip of the limb. Although each hair measures only 0.12 mm. *this row doubtless is homologous with the comb of the Theridiidae*, since the position of the row is in each case the same and the structure of the hair, if we disregard its length, very much alike. This brings the family of the Pholcidae, originally regarded as a subfamily of the Theridiidae and later separated from the latter family, into closer relation with it again. Such opinion is further substantiated by the fact that other representatives of the Family Pholcidae show similar conditions. In Spermophora meridionalis the row consists of 16 hairs one of which is represented in Fig. 12. In two species of Modisimus from Jamaica I find this row represented by hairs of the type found in the other eight rows, but the distal four hairs show distinct teeth or spines characteristic for the combhair. In Pholcus tipuloides the whole row differs from that of Pholcus phalangoides, resembling more the lower end bristle of this latter species and thus constituting a character in itself sufficient to keep the two species apart. On the other hand neither Hypselistes (Erigone) florens, nor any of the five common species of Linyphia examined, show anything of the kind.

II. On the Muscular System of the legs.

The muscular system of the legs in spiders has been studied several times. The last paper of importance was that by Paul Gaubert in the Annales des Sciences Naturelles, Vol. 13, 1892. Yet neither his studies, nor those of Börner have brought the question to a conclusion. Moreover they contain errors. Thus one of the muscles of the patella was entirely overlooked and another in the tibia wrongly described and in consequence its function misunderstood.

I used as material transparent legs of small spiders. They can be studied in life, or after enclosure in glycerin, or by fixing the whole leg in picric acid which stains intensely and permanently yellow the muscles and by enclosing it then in canada balsam. Side views were controlled by dorsal and ventral views of corresponding segments. In some cases sections were necessary and the paraffin-method was used. Besides small spiders I have also studied the muscular system in several very large spiders, such as Heteropoda venatoria, Ctenus malvernensis sp. n., Lycosa carolinensis, Pachylomerus nidulans and unidentified species of Eurypelma. In all these the muscles can be isolated with the aid of dissecting instruments even without a magnifying glass.

Coxa. Enclosed in the coxa are five muscles one of which really belongs to the trochanter and will be described with the other muscle of that segment. The four muscles belonging to the coxa are: 1. *M. flexor trochanteris* (Fig. 3, fl. tr.) This muscle arises from the episynaxial surface of the coxa and partly from the chitinous septum which occupies the synaxial plane of the coxa and divides its anterior two thirds into an upper and lower half. The muscle is inserted with a tendon into the proximal epi-edge of the trochanter. 2. *M. extensor trochanteris* (Fig. 3. ex. tr.), the antagonist of the preceding arises from the hyposynaxial surface of the Coxa and partly from the septum. Its tendon is inserted into the proximal hypo-edge of the trochanter. 3. *M. promotor trochanteris*, a broad muscle with parallel fibres which arise from the prosymmetrical surface of the Coxa and are inserted without tendons into the proximal prosymmetrical edge of the trochanter. 4. *M. retractor trochanteris* (Fig. 3. r. tr.) the antagonist of the promotor occupying the symmetrical position on the retro-side.

Trochanter. Two muscles are enclosed in the trochanter. 1. *M. flexor femoris longus* (Fig. 3. fl. f. l.) a weak muscle which arises from the coxal septum and is inserted by means of a tendon into the proximal epi-edge of the femur. Gaubert, who calls this muscle "abaisseur," describes it as arising from the inferior (Hyposynaxial of my terminology) surface of the coxa, not from its septum. I think that in some cases I have seen fibres running in that direction, but I am not positive about it. The function of this muscle is certainly not that of the common flexor but it is not an "abaisseur" (depressor), since it probably helps the flexor bilobatus to lift the femur and at the same time tends to bring the whole femur nearer towards the trochanter. 2. *M. flexor femoris bilobatus* (Fig. 3. fl. f. b.) consists of two symmetrical halves arising from the hyposynaxial surface of the trochanter. Its numerous short tendons are inserted close together into the same edge with the flexor longus.

Femur. Enclosed in the femur we find two muscles closely resembling those of the trochanter. 1. *M. flexor patellae longus* (Fig. 3. *fl.* p. l.) has two proximal tendons one of which arises from the distal end of the hyposynaxial surface of the trochanter and the other from the corresponding proximal end of the femur. The fibres soon form one spindle-like muscle which is inserted with a long tendon into the proximal hypo-edge of the patella. 2. *M. flexor patellae bilobatus* (Fig. 3. fl. p. b.) is in every respect homologous with the corresponding muscle of the trochanter, but as the flexor femoris *raises* the femur, while the flexor patellae *lowers* the patella together with the tibia, the two homologous muscles arise from the opposite surfaces. It is the articulation of the segments that determines the position of muscles. The musculus flexor patellae bilobatus consisting of two symmetrical halves arises therefore from the entire episynaxial surface of the femur and its numerous short tendons are inserted close together into the proximal hypo-edge of the patella on both sides of the long flexor.

Patella. The articulation of the patella with the tibia is such as to allow of scarcely any motion. Notwithstanding this we find three muscles in the patella. Two of these are symmetrical and consist of parallel fibres arising from the episynaxial and the pro- and retrosymmetrical surfaces of the segment. Each separate fibre is inserted apparently without a tendon into the proximal pro- and retro-edges of the tibia. These two muscles are: 1, *M. promotor tibiae*, and 2, *M. retractor tibiae* (Fig. 3. r. t.) The third muscle which is also to all appearances functionless is 3, *M. flexor tibiae*. It arises from the proximal end of the episynaxial surface of the patella and is conical in shape. Its long cylindrical tendon is inserted into the middle of the proximal hypo-edge of the tibia. This muscle is entirely overlooked by previous investigators although it may easily be found in spiders of different families and all sizes.

Tibia. The muscles of the tibia are in every respect homologous with those of the femur. A number of fibres arise from the proximal surface of the patella without however forming a tendon, and join in the tibia those fibres which arise by means of a tendon from the proximal hypo-edge of this latter segment. Together they form the 1.—*M. flexor metatarsi longus* (Fig. 3. fl. m. l.) which is inserted with a long tendon into the middle of the proximal hypo-edge of the metatarsus. 2, *M. flexor metatarsi bilobatus* (Fig. 3. fl. m. b.) is composed of two symmetrical halves and arises from the entire episynaxial surface of the tibia. Its numerous short tendons are inserted closely together on both sides of the tendon of the long flexor. The description of this muscle given by Gaubert is entirely wrong and I am not able to comprehend what has brought him to the conclusion that its point of insertion is on the dorsal (episynaxial) surface of the metatarsus and that this muscle is therefore an extensor. There is no extensor of the metatarsus.

METATARSUS. Enclosed in the metatarsus are two muscles, one of which is the antagonist of the other. 1, *M. flexor unguium* (Fig. 3. fl. u.) arises from the proximal surface of the metatarsus and receives additional fibres which arise from the distal end of the episynaxial surface of the tibia. Its long, thin tendon traverses the metatarsus and tarsus and is inserted into the base of the claws. 2, *M. extensor unguium* (Fig. 3. ex. u.) arises from the proximal epi-edge of the metatarsus and is inserted by means of a long and thin tendon which runs above and parallel to that of the flexor into the base of the claws above the latter.

TARSUS. The tarsus has no muscles and encloses merely the two tendons above mentioned.

In reviewing the muscular system of the legs in spiders we observe that its characteristic feature is the absence of extensors in the majority of segments. Only the coxa and the metatarsus enclose extensors.[1] The function of the extensors is evidently transferred in the other segments upon the hypodermis forming a thin elastic membrane over each joint. The homology of the muscles enclosed in the femur and tibia is too apparent to admit of doubt, and I believe that it can be extended to the muscles

1. In the second volume of his text-book of experimental zoölogy, which has just appeared, Przibram reproduces Frédéricq's diagram of the muscular system of a spider-leg. Evidently misled by Garber's old interpretation of the muscular system of appendages in Arthropods, he figures a flexor and an extensor in every segment of the limb. However, even a superficial examination of the articulations cannot fail to show that his supposed extensors are in reality flexors. If he had noticed that the axes of the patellar and metatarsal articulations lie not on the ventral side of the limb, but in its episynaxial (dorsal) surface, he would have escaped this error.

enclosed in the trochanter. Such conception is certainly true in the case of the flexor bilobatus. As for the flexor femoris longus, some doubt may be expressed as to its homology with the corresponding flexors of the patella and metatarsus. But the shortness of the trochanter and the difference in articulation may be held responsible for the fact that the flexor femoris longus arises from another surface than its homologs. The muscles of the patella are doubtless homologous with those of the coxa with that exception that there is no extensor tibiae. We must however remember that an extensor tibiae would be of still less use than the flexor, since the patella has a special tooth at its distal end interlocking with the tibia. This interlocking device prevents the tibia from being raised apart from the patella, the only functioning "knee" articulation being that between the femur and the patella.

EXPLANATION OF THE FIGURES (PLATE IV.)

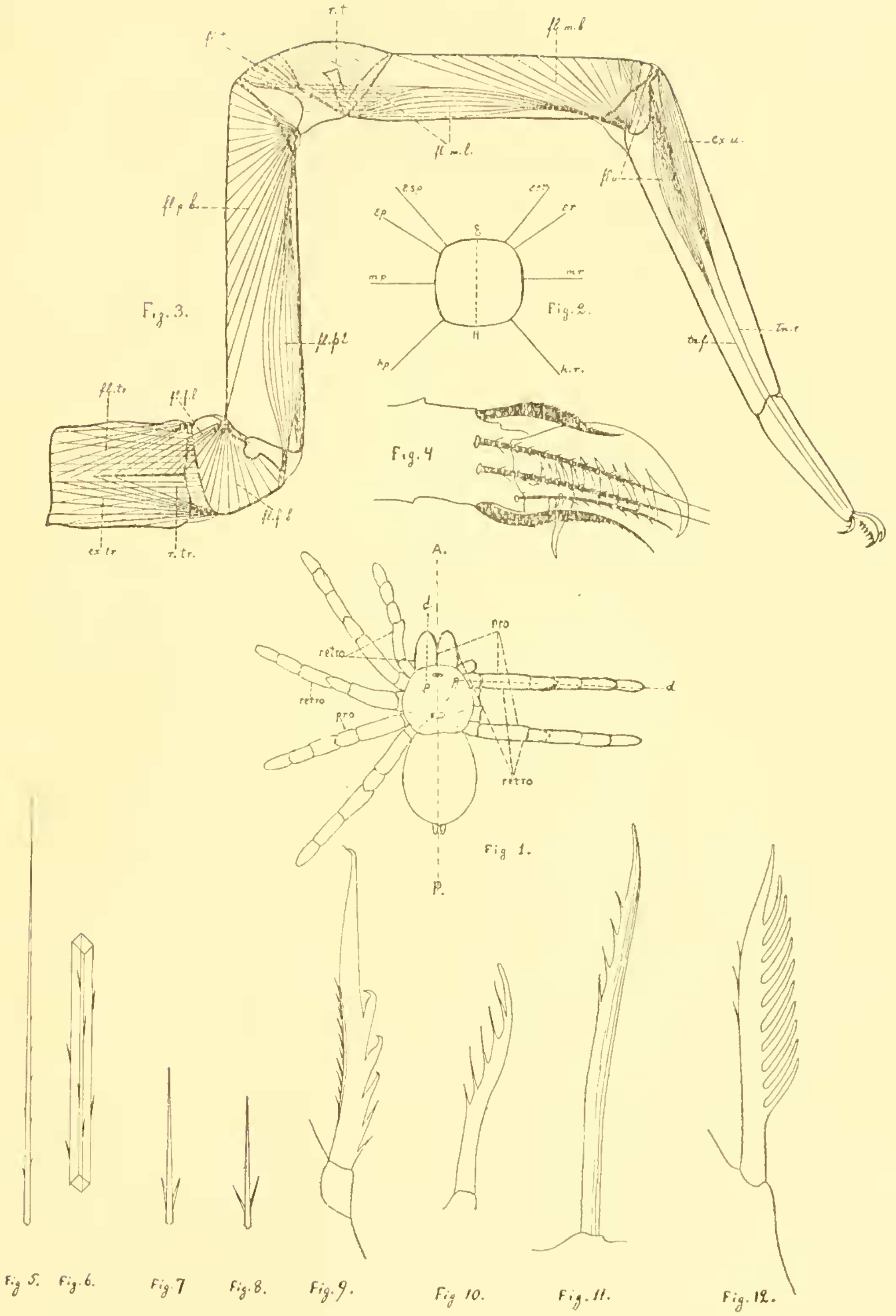
1. Diagram of a spider showing the axis of complex symmetry, AP, and the planes of symmetry of the legs, pd, and of the chelae. The second and third legs on the right side are removed. The figure represents the dorsal surface of the spider and the legs are extended in such a manner that the surface of the paper represents the episynaxial surface.

2. Diagram representing a cross section of the leg of Pholcus phalangoides. EH, the plane of symmetry. It is understood that the observer sees the cross section in looking from the body of the spider towards the end of the leg. In consequence it is evident from the letters accompanying the diagram that it is a cross section of a right leg. In a left leg the two halves are reversed. ESP, proepisynaxial; ESR, retoepisynaxial; EP, apipro, ER, epiretra; MP, middle pro; MR, middle retro; HP, hypo pro; HR, hyporetro hair.

3. The muscular system of a spider leg. fl. tr., flexor trochanteris; ex. tr., extensor trochanteris; r. tr., retractor trochanteris. Its antagonist, the M. promotor trochanteris, runs parallel to the retractor and cannot therefore be represented on the diagram. One must imagine that it was removed for the purpose of showing the other muscles. fl. f. l., flexor femoris longus; fl. f. b., flexor femoris bilobatus; fl. p. l., flexor patellae longus; fl. p. b., flexor patellae bilobatus; fl. t., flexor tibiae; r. t., retractor tibiae. Its antagonist the M. promotor tibiae runs parallel to the retractor and could not be represented in the diagram. fl. m. l., flexor metatarsi longus; fl. m. b., flexor metatarsi bilobatus; flu., flexor unguium; ex. u., extensor unguium- tn. f., the tendon of the flexor; tn. e., the tendon of the extensor.

4. The bristles surrounding the claws of Pholcus phalangoides. The heavy upper and lower bristles are single. Three bristles corresponding with the three other bristles of the figure are situated on the other side of the claws and can not be represented.

5—11. Hairs on the legs of Pholcus phalangoides. 5, on femur, patella, tibia and the two proximal thirds of metatarsus. 6, a part of the same hair stronger magnified. 7, a hair from the distal end of the metatrasus; 8, a hair from the tarsus. 9, the combhair of the fourth tarsus. 10, one of the few erect, scattered hairs on the tarsus. 11, the same from the metatarsus. 12, one of the combhairs of Spermophora meridionalis.



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